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PARTHENOGENESIS AND CROSSING-OVER IN THE GROUSE LOCUST APOTETTIX[1]

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INTRODUCTION

THERE have been found among the grouse locusts, genus *Paratettix*,[2] in nature, fourteen factors for color patterns, all in one series of multiple allelomorphs. A fifteenth factor, a modified S, in the same series, has originated in the laboratory by means as yet not understood. Another factor, θ, for melanism, discovered in nature, has been found to segregate independently of the multiple allelomorph group (Nabours, '14, '17). Still another factor, ϕ, for red-all-over, yet to be described, also from nature, behaving precisely as does θ, though segregating independently of both it and the multiple allelomorph series, has been bred in considerable numbers. In one species of the genus *Tettigidea*,[3] bred in our laboratory, there have been described a series of five multiple allelomorphic factors for patterns, and an independently segregating color factor of the behavior of θ, or ϕ, in *Paratettix* (Bellamy, '17). In these experiments, involving several hundred kinds of matings and many thousands of individuals, with only the two exceptions, both as yet unexplained, segregation has taken place as expected.

Among another genus, *Apotettix*,[4] of the grouse locusts there have been discovered in nature eleven factors for color patterns, all in the same series, but evidently only a few, if any, are allelomorphs. Pending further consideration, the patterns are designated as AA, GG, KK, MM, OO, RR, TT, WW, XX, YY and ZZ, respectively (all conspicuous, except AA which is of a mottled gray ground color and well protected). These patterns are as sharply defined and distinct, each from any other, as are those of *Paratettix.* Any two make a readily recognizable hybrid pattern, with the elements of each parent pattern seemingly equally represented, except that the part of a hybrid pattern produced by the factor A, when it is a member, is less clearly perceived, and such hybrids can not be, in every case, superficially distinguished from the pure, or homozygous, pattern of the more apparent member. For instance, it requires trained and careful scrutiny to distinguish between AK and KK, AW and WW, AY and YY, etc. It appears that the pattern AA, if it be the result of only the one factor, is quite different from the others, not only in its manifestation in the hybrid of which it may be a member, but also, as will be shown later, in that it appears to result from crossing-over among the others. On the other hand, KW, KY, WY, and most other hybrid patterns not containing A as a member are sharply distinct, each making a composite picture of both components. Even in case of linkage, where three, four or more factors are combined, the individual presents the composite appearance of all the patterns involved. For example, in $K\overset{\frown}{MR}$, $\overset{\frown}{KM}R$ or $\overset{\frown}{KR}M$, $K\overset{\frown}{YZ}$ and $\overset{\frown}{KR}\overset{\frown}{YZ}$ individuals all the patterns concerned are clearly visible and apparently equally represented. In respect to representation of patterns in the hybrids, as well as in the actual resemblance of a few of the patterns, there is striking parallelism between some of the members of this genus and some of those of *Paratettix.*

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[1] Paper 25 from the Zoological Laboratory, Kansas Agricultural College and Experiment Station.

[2] *Paratettix texanus* Hancock. Kindly identified by both Dr. J. L. Hancock and Mr. Jas. A. G. Rehn.

[3] *Tettigidea parvipennis pennata* Hancock.

[4] Identified by Mr. Rehn as *Apotettix eurycephalus* Hancock, and by Doctor Hancock as follows: "nearer the Mexican species *Apotettix convexus Morse,* than the nearly allied Texan species, *Apotettix eurycephalus* Hancock. Inasmuch as you have used material from both Texas and Mexico in your experiments, it is possible you have hybridized the two." The natural history of this group has been described (Hancock '02).

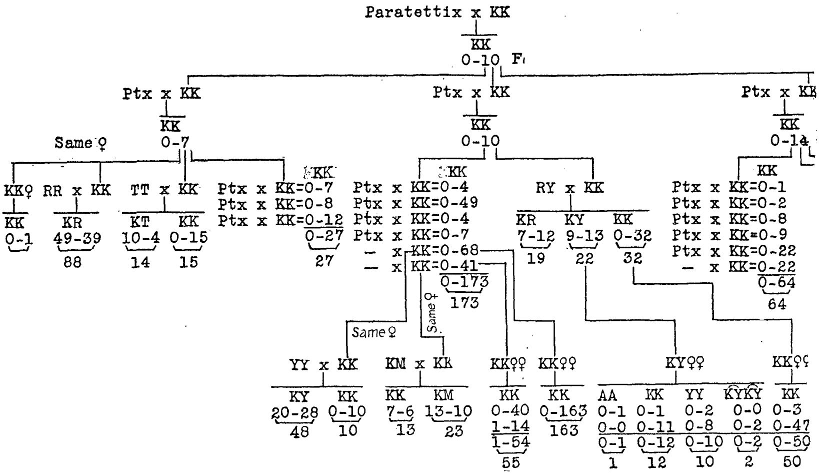
However, as already suggested, in contrast with the inheritance behavior in *Paratettix,* most of the factors in *Apotettix* show from small to considerable percentages of crossing-over. The discovery of crossing-over, with the further disclosure that these forms breed parthenogenetically, as well as bisexually, prompts me to submit a preliminary report in advance of a more extended presentation of the data and illustrations which can not be made ready this year.

The Adams fund has cared for the expenses, and I have had the generous and open-minded support of director, now president, W. M. Jardine. Mr. A. W. Bellamy gave effectual assistance during the earlier stages of the experiment.

PARTHENOGENESIS AND CROSSING-OVER IN THE FEMALE

The discovery of parthenogenesis in *Apotettix* was the result of attempts at cross-breeding the members of this genus with those of the genus *Paratettix*. It was observed that when an *Apotettix* male was used with a *Paratettix* female no progeny ever resulted, but the female of the reciprocal gave offspring, exclusively females, and of her own color pattern if she were homozygous, or segregated into her components and crossovers if she were heterozygous. Then it was soon ascertained (see chart) that the *Apotettix* females which had never been exposed to males of any kind at any time behaved in this respect precisely as did those exposed to *Paratettix* males. Copulation between members of the two genera was never observed. Confirming these observations, Dr. J. L. Hancock kindly examined specimens for me and concluded that on account of structural differences the members of the one group could not mate with those of the other.

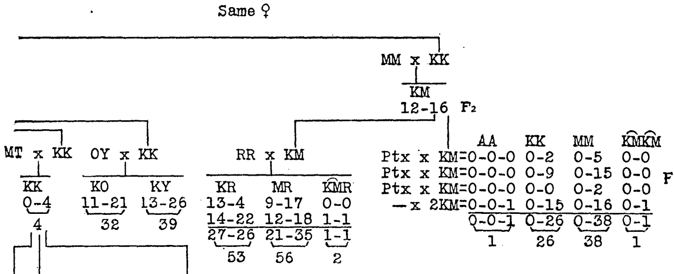
The chart illustrates a portion of the experiment which definitely determined that parthenogenesis occurs. It also shows crossing-over in the females. Following the chart, the first KK female, exposed to a *Paratettix* male of strongly contrasting pattern, produced 10 offspring, all females and of her own pattern. Three of these F_1

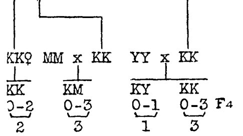


individuals were separately exposed to *Paratettix* males and gave 7, 10 and 14, respectively, and again all were KK females like the female parents and grandparent. One of these F_1 females was subsequently mated to a male of the strongly contrasting pattern MM, of her own genus, and then she produced 12 males and 16 females of the composite pattern KM.

From left to right, in F_2, a female KK was mated to an RR male and gave, in F_3, 49 ♂♂ : 39 ♀♀ of the intermediate KR pattern. About three weeks after the death of the male this KK female was removed to another cage, where she produced a few offspring, the only one recorded being a KK female. The next F_2 KK female was mated to a TT male of a strongly contrasting pattern. She produced 10 ♂♂ : 4 ♀♀ of the hybrid pattern KT, and 15 KK's, all females and without a trace of the TT pattern. The following three F_2 KK females were placed with *Paratettix* males and produced 7, 8 and 12 KK females, respectively. The next four F_2 KK females were also exposed to *Paratettix* males, and gave 4, 49, 4 and 7 offspring, all like the female parents; while the remaining two sisters, without exposure to males of any kind at any time, gave, in F_3, 68 and 41 KK females, respectively.

One of these, the one having produced 68 offspring





Explanation.

Ptx=Paratettix male. Males on the left; females on the right., 0-27=no males:27 females. 0-0-1=Sex not determined. 49-39=49 males:39 females. All other letters refer to factors in Apotettix and patterns.

parthenogenetically, was mated to a YY male and gave KY 20 ♂♂ : 28 ♀♀ and 10 KK ♀♀ without a trace of the YY pattern. The other F_2 KK female, which had given 41 offspring parthenogenetically, when mated to a KM male, gave KK 7 ♂♂ : 6 ♀♀, and KM 13 ♂♂ : 10 ♀♀. It is obviously impossible to determine if all the KK offspring from this mating were produced bisexually, or some of them parthenogenetically. However, since parthenogenetically produced individuals are, with rare exceptions, females, the result is somewhat checked by the proportion of 7 ♂♂ : 6 ♀♀. From the 68 F_3 offspring several females were allowed to reproduce without exposure to males of any kind at any time, and 163 KK females resulted in F_4. From the 41 KK F_3 individuals one which had never associated with any male gave 40 KK females in F_4, and another, also parthenogenetically, gave 14 females and 1 male, all KK's.

The following F_2 KK female was mated with an RY male and gave KR 7 ♂♂ : 12 ♀♀, KY 9 ♂♂ : 13 ♀♀, and 32 ♀♀ of the pattern of the KK parent. Two of these F_3 KK females were further tested parthenogenetically and produced, in F_4, a total of 50 offspring, all like themselves. Two of the KY ♀♀ were bred parthenogenetically and gave, both combined, 1 AA : 12 KK : 10 YY : 2 $\widehat{KY}\widehat{KY}$, all females, thus exhibiting the crossovers AA and $\widehat{KY}\widehat{KY}$, as well as the expected segregates KK and YY.

The five next F_2 KK females placed with *Paratettix* males produced 1, 2, 8, 9 and 22 offspring, respectively, all KK females. The sixth female of this group, exposed to no male whatsoever, behaved precisely as did those individuals which had been with *Paratettix* males. Another of these F_2 KK females was placed with an MT male with 4 KK female offspring resulting in F_3, none evidencing any M or T part in the parentage. Three of these were bred further and gave offspring in F_4 as follows: one, without any male, 2 KK females; the second, mated to an MM male, 3 KM females showing the male parentage unmistakably; and the third, mated to a YY male, 1 KY female showing male parentage clearly, and 3 KK females indicating none of the male characteristics and plainly parthenogenetic. On account of the extremely small numbers involved, I suggest there is no special significance to the absence of males in the two last described matings. An eighth F_2 KK female, of this group, was mated to an OY male and gave KO 11 ♂♂ : 21 ♀♀ and KY 13 ♂♂ : 26 ♀♀.

The following two matings show RR males mated to KM females and giving KR 27 ♂♂ : 26 ♀♀, MR 21 ♂♂ : 35 ♀♀ and the crossovers $\overset{\frown}{KM}$R 1 ♂ : 1 ♀. Three of the KM females were placed with *Paratettix* males, but the offspring exhibited no more evidence of male parentage than those produced by the two KM sisters without exposure to any male. The combined result from the five KM sisters was AA 1 : KK 26 : MM 38 : $\overset{\frown}{KM}\overset{\frown}{KM}$ 1, all females, except that the sex of the AA individual was not determined. As in the case of the KY females already noted, this furnishes a very interesting exhibition of segregation as well as crossing-over in parthenogenetic individuals.

Subsequently from KK females, individually and in groups, but not exposed to males of any kind at any time, there have been given 2,726 female and 4 male offspring, all KKs, some of them having arrived at the fifth parthenogenetic generation. Including the KK females represented in the chart, and others exposed to males without effect, there have been produced parthenogenetically from KK females, a total of 3,289 females and 5 males, all of the KK pattern. Other females than KK (some of the data presented below) have produced 1,181 females and 2 males, making a total of 4,470 females and 7 males of various patterns produced parthenogenetically (August 1, 1918). Individuals of all the patterns, except AA which has not been adequately tested, have given offspring by parthenogenesis. It is not known if any one breeds in this way more readily than any other, the KK's having been used up to the present time more than the rest. Furthermore, it has not been determined whether, or not the capacity for parthenogenesis is in any sense an inheritable character. There are, however, great differences among individuals in this respect, even from the same F_2, or F_3, parthenogenetic batch.

Note: ♂♂ on the left.
♀♀ on the right.

(1)
MM ♀ ♀

	MM
	0–1
	0–1
	0–7
	0–12
	0–15
	0–37
	0–23
Total	0–96

(2)
RR ♀ ♀

	RR
	0–1
	0–16
	0–61
	0–7
	0–24
	0–35
	2–24
Total	2–168

(3)
YY ♀ ♀

	YY
	0–2
	0–4
	0–5
	0–22
	0–8
Total	0–41

(4)
$\widehat{YZ}\widehat{YZ}$ ♀ ♀

	$\widehat{YZ}\widehat{YZ}$
	0–18
	0–7
	0–19
Total	0–44

(5)
$\widehat{MR}\widehat{MR}$ ♀

	$\widehat{MR}\widehat{MR}$
	0–1
	0–16
Total	0–17

(6)
KM ♀ ♀

	AA	KK	MM	$\widehat{KM}\widehat{KM}$
	0–0–0	0–1	0–3	0–1
	0–0–0	0–5	0–5	0–0
	0–0–0	0–13	0–12	0–0
Total	0–0–0	0–19	0–20	0–1
From Chart	0–0–1	0–26	0–38	0–1
Total	0–0–1	0–45	0–58	0–2

(7)
KY ♀ ♀

	AA	KK	YY	$\widehat{KY}\widehat{KY}$
	0–0	0–6	0–2	0–0
	0–0	0–3	0–3	0–0
	0–0	0–1	0–0	0–0
	0–0	0–4	0–9	0–0
Total	0–0	0–14	0–14	0–0
From Chart	0–1	0–12	0–10	0–2
Total	0–1	0–26	0–24	0–2

(8)

K$\overset{\frown}{YZ}$ ♀ ♀

	KK	$\overset{\frown}{YZ}\overset{\frown}{YZ}$	$\overset{\frown}{KY}\overset{\frown}{KY}$	ZZ
	0–3	0–11	0–0	0–1
	0–14	0–8	0–1	0–1
	0–4	0–6	0–1	0–1
Total	0–21	0–25	0–2	0–3

(9)

MR ♀

AA	MM	RR	$\overset{\frown}{MR}\overset{\frown}{MR}$
0–2	0–11	0–4	0–2

A few other results from breeding *Apotettix* females parthenogenetically are given in the above tables, which also include the segregation and crossing-over in the KY and KM females shown in the chart.

Further crossing-over is indicated in the parthenogenetic K$\overset{\frown}{YZ}$ females (8) and the MR female (9). The latter indicates more than 21 per cent. of crossing-over, but the total crossing-over shown in 296 offspring from MR females, produced both bisexually and parthenogenetically, amounts to only 20, or less than 7 per cent. A few other simple hybrid females, some parthenogenetically and others bisexually, have produced crossovers as follows:

From GM females 279 individuals with 11 crossovers, about 4 per cent.
From KM females 517 individuals with 5 crossovers, about 1 per cent.
From KY females 205 individuals with 12 crossovers, about 6 per cent.
From RY females 33 individuals with 3 crossovers, about 10 per cent.
From TY females 70 individuals with 8 crossovers, about 12 per cent.
From RT females 125 individuals with no crossovers.

There is every indication that as the numbers available become larger these percentage figures will be different; therefore it seems inadvisable to project at this time even a tentative diagram illustrating crossing-over percentages.

Crossing-over in the Male

Crossing-over in the females, in parthenogenetic as well as bisexual reproduction, is shown in the chart, and tables (1–9), and there are numerous other cases to be presented later in both bisexual and parthenogenetic breeding. While it appears that the crossovers in the females greatly exceed those in the males, the data are as yet insufficient to justify a final judgment. A few of the considerable number of cases of crossing-over in males are herewith given:

(10)

$A\widehat{YZ} \times AK$

AA	AK	$A\widehat{YZ}$	$K\widehat{YZ}$	AZ
3–2	3–2	2–3	6–1	0–1
5	5	5	7	1

(11)

$O\widehat{TY} \times KK$

KO	$\widehat{KT}Y$	KT
9–12	11–17	2–1
21	28	3

(12)

MR × GK

GM	GR	KM	KR	$K\widehat{MR}$
1–4	3–5	1–5	1–2	0–1
5	8	6	3	1

(13)

KM × RR

KR	MR	$\widehat{KM}R$	AR RR
6–7–5	3–14–4	0–1	0–2
18	21	1	2

(14)

$\widehat{KY}M \times RT$

MR	MT	$\widehat{KY}R$	$\widehat{KY}T$	$\widehat{KM}T$
8–15	14–9	16–20	14–4	0–1
23	23	36	28	1

The KM × RR mating (13) is of interest and a sample of a frequent occurrence. The $\widehat{KM}R$ individual, of unmistakable pattern, could not be accounted for otherwise than by assuming crossing-over in the male, but since AR and RR were so much alike and were not bred further, we can not know whether both of these were AR, the A gamete coming from crossing-over in the male, or whether they were RR produced parthenogenetically by the RR parent, or one was produced by the former and the other by the latter method.

Discussion

Are the female gametes in this group of grouse locusts all of the same kind with respect to the necessity of fertilization, or do some of them require the spermatozoon, in order to develop, and others not? The latter situation is suggested by the fact that mated individuals frequently reproduce bisexually and parthenogenetically at the same time. Also, often, when an individual which has been reproducing parthenogenetically is mated she thenceforth gives offspring, some exhibiting, and others not, male parentage. In an unmated female perhaps the eggs that require fertilization disintegrate either before or after oviposition. (The eggs are oviposited in the ground. This matter can be, and is being, investigated.) On the other hand, it as often happens that when an individual reproducing parthenogenetically is mated she thenceforth gives offspring all showing male parentage. Also, though less readily, a mated female reproducing exclusively bisexually, when placed to herself, will, after a few weeks, give offspring parthenogenetically. Although the end result data which might give light on this point have not as yet been adequately developed, I venture the suggestion that with respect to the need of fertilization the mature eggs are approximately the same, and that it is the time of the entrance of the spermatozoon which determines the matter. If a spermatozoon enters the egg at the proper stage of its maturation the pronuclei unite; if no spermatozoon enters, or one enters too late, the egg either proceeds parthenogenetically, or fails to develop altogether.

The diploid number of chromosomes in the *Apotettix* female appears to be fourteen. This number has been clearly demonstrated in the late metaphase plate of an oogonial division in an individual derived bisexually. In a preparation of somatic cells of a female produced parthenogenetically, nine apparently whole chromosomes and some fragments were observed in one (Mr. A. H. Hersh, unpublished.) The females of some other members of the Tettigidæ have fourteen chromosomes (Robertson, '16). In some forms of the Tettigidæ the males have been shown to have thirteen chromosomes as the complete number (Harman, '15, and Robertson, '16).

The "maneuvers of the chromosomes" theory of Morgan may very well account for the observed end results presented in this paper, though the possibility of some other explanation is not by any means excluded. Even if the results herein entitled "crossing-over" should at some time be found actually not to be connected with the maneuvers of the chromosomes, the term might still be retained as an adequate expression of whatever does occur. The discussion of the mechanism, physiological processes, or both, involved in the parthenogenesis must await further investigation.

In nature, individuals of the pattern AA, of a mottled gray ground color, in striking contrast with, and much less conspicuous than, the rest, exceed in numbers all the others combined. This situation has been accounted for in the past by the assumption that the brilliant patterns rendered the individuals possessing them so conspicuous that they more readily fell prey to enemies, while the inconspicuous and protected AA individuals were largely unmolested. Now, since it has been demonstrated that crossing-over among the forms of conspicuous patterns produces the A gametes as well, the cause of the preponderance of AA patterns in nature may, in part at least, call for an entirely different explanation. AA may be the primitive form and the others have originated from it, by mutation or in some other way. The form AA seems to correspond to the so-called "normal" or "wild type," though all the others have also been found exclusively in nature, none (in *Apotettix*) having so far originated in the laboratory.

CONCLUSIONS

1. Through complete isolation of females from males of any kind, in some cases for as many as three generations, and, in addition, by genetic behavior, it has been demonstrated that these forms of *Apotettix* are gynogenetically, except rarely parthenogenetic (tychoparthenogenetic).
2. Segregation is demonstrated as occurring in heterozygous individuals reproducing by parthenogenesis, as well, and apparently to the same extent, as in those females reproducing bisexually.
3. Crossing-over is demonstrated as occurring in heterozygous individuals reproducing by parthenogenesis, as well, and apparently to the same extent, as in those females reproducing bisexually.
4. Crossing-over occurs in the male, as well, but apparently not to the same extent, as in the female.

LITERATURE CITED

Bellamy, A. W. 1917. Studies of Inheritance and Evolution in Orthoptera, IV. *Journal of Genetics,* Vol. VII, No. 1.

Hancock, J. L. 1902. The Tettigidae of N. A. Chicago.

Harman, Mary T. 1915. Spermatogenesis in Paratettix. *Biol. Bulletin,* Vol. XXIX, No. 4.

Morgan, T. H., and others. 1915. Mechanism of Mendelian Heredity. New York.

Nabours, Robert K. 1914. Studies of Inheritance and Evolution in Orthoptera, I. *Journal of Genetics,* Vol. III, No. 3.

Nabours, Robert K. 1917. Studies of Inheritance and Evolution in Orthoptera II and III. *Journal of Genetics,* Vol. VII, No. 1.

Robertson, W. R. B. 1916. Chromosome Studies I. *Jour. Morphology,* Vol. XXVII, No. 2.